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Pattern specificity of human visual motion processing

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Abstract

Visual motion processing is strongly susceptible to adaptation. A variety of patterns have been used as stimuli in previous studies. Three of these, namely random dots, barcode-like gratings, and sinusoidal gratings, were compared in the present study using motion-onset visual evoked potentials (VEPs). We assessed the effects of the adaptation pattern and the test pattern to which the VEP is recorded. Furthermore, we evaluated the interaction between both, i.e. whether differences between adaptation and test pattern affect the response. Isodirectional and antidirectional adaptation were used to differentiate between the actual motion adaptation and associated flicker adaptation. Motion adaptation was almost 2.5-fold stronger ($p < 0.01$) if the same rather than different pattern types were used for both adaptation and test. This implies that separate neural populations are involved, suggesting the presence of pattern-tuned motion mechanisms.

Keywords: Motion processing; Pattern; Adaptation; Cortex; Human; VEP

1. Introduction

Motion is an intensively investigated field of visual processing. Motion-processing neural mechanisms in the strict sense are defined by their direction-selectivity. A key issue in motion processing is adaptation. It results in a reduced neural response if subjects have viewed a motion stimulus for a prolonged period of time, i.e. during several seconds (Hoffmann, Dorn, & Bach, 1999).

There is a consensus in literature that area MT (V5) or structures in its vicinity are involved in motion processing in humans while reports about the relevance of other areas are less consistent (e.g., Ahlfors et al., 1999; Anderson, Holliday, Singh, & Herding, 1996; Chawla, Phillips, Buechel, Edwards, & Friston, 1998; Dupont, Orban, De Bruyn, Verbruggen, & Mortelmans, 1994; ffytche, Guy, & Zeki, 1995; Hollants-Gilhuijs, de Munck, Kubova, van Royen, & Spekreijse, 2000; Howard et al., 1996; Huk, Doughterty, & Heeger, 2002; Probst, Plendl, Paulus, Wist, & Scherg, 1993; Schellart, Trindade, Reits, Verbunt, & Spekreijse, 2004; Shulman, Schwarz, Miezin, & Petersen, 1998; Smith, Greenlee, Singh, Kraemer, & Hennig, 1998; Uusitalo, Jousmaki, & Hari, 1997; Watson et al., 1993).

There is evidence that MT neurons in monkeys are sensitive to a particular speed rather than a temporal frequency, while V1 neurons are sensitive to specific spatial and temporal frequencies (Perrone & Thiele, 2001). This assumption is also supported by fMRI experiments that investigated the processing of pattern motion in humans (Huk & Heeger, 2002). Correspondingly, many models of human motion detection propose two stages, one responding to local motion signals and the other integrating these responses over a larger region (e.g., Braddick & Quian, 2001; Mather & Harris, 1998). Such a detector for spatially global motion is likely to respond to a large variety of patterns. It is not clear, though, how different patterns would affect the absolute activity of

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speed-tuned neurons, which might still depend on pattern properties. Monkey fMRI studies in fact suggest that differences between random dots and random lines exist (Vanduffel et al., 2001).

Motion visual evoked potentials, in particular motion onset potentials, have been used extensively to study the processing of motion in the visual system. They are dominated by a negativity (N2) around 150–200 ms, which has been suggested to have its origin in area MT (Probst et al., 1993), possibly with contributions from V3/V3A or nearby (Schellart et al., 2004). The N2 is highly susceptible to adaptation (Bach & Ullrich, 1994; Göpfert, Müller, & Hartwig, 1984; Göpfert, Müller, Markwardt, & Schlykowa, 1983; Schlykowa, van Dijk, & Ehrenstein, 1993).

First-order visual motion is always associated with local temporal changes in luminance. Recent studies have revealed that two distinct adaptation effects occur in the motion VEP, reflecting direction-specific and non-specific neural mechanisms, respectively (Heinrich & Bach, 2003; Hoffmann, Unsöld, & Bach, 2001; Maurer & Bach, 2003). For simplicity, we will subsequently use the terms 'motion mechanisms' and 'flicker mechanisms'. The latter represent any non-direction-specific neural circuits, including those that are sensitive to simple temporal modulations in luminance or respond equally to both motion directions, e.g. those already described by Hubel and Wiesel (1959, 1962). An earlier positivity (P1) around 100 ms after stimulus onset, i.e. preceding the N2, is also affected by motion adaptation. However, although P1 exhibits a dependence on adaptation direction, it does not appear to be a motion-specific component itself: In contrast to N2, P1 increases with increasing depth of motion adaptation (Bach & Ullrich, 1994; Hoffmann et al., 1999) and is presumably associated with the fact that the motion-onset VEP is the summed potential evoked by different processes leading to P1 and N2 (Bach & Ullrich, 1997; Kubova, Kuba, Spekreijse, & Blakemore, 1995). Overlapping in time, these potentials interact as they superimpose in the VEP and consequently a decrease of N2 would result in an increase of P1.

A broad range of stimulus patterns, characterized mainly by their Fourier spectra, have been used previously to investigate motion processing. In the present study we addressed two main questions using motion-onset VEPs: (a) How do different patterns affect the motion response? (b) Does it matter whether the pattern used for adaptation is the same as the one used to record the motion response? If yes, it would suggest that the neural substrate of motion processing is at least partly pattern-specific. This approach, sometimes referred to as "selective adaptation", has been applied successfully in several recent studies to investigate neural properties motion-processing mechanisms not directly accessible due to limitations in the spatial resolution of the VEP (Heinrich, van der Smagt, Bach, & Hoffmann, 2004; Maurer, Heinrich, & Bach, 2004), but has also been used in other fields such as fMRI experiments on pattern and object processing (e.g., Buckner & Koutstaal, 1998; Grill-Spector & Malach, 2001; Kourtzi, Erb, Grodd, & Bulthoff, 2003). Taking the motion aftereffect as an indicator, some psychophysical studies suggest that adaptation exhibits a considerable degree of spatial frequency selectivity (Bex, Verstraten, & Mareschal, 1996; Cameron, Baker, & Boulton, 1992). Recent work by Fang and He (2004), though, demonstrates that squarewave patterns and sinewave patterns are equally good motion adaptors if either of them is used as a test pattern.

2. Methods

2.1. Stimulus

Stimuli were generated by a PowerMacintosh G4 and displayed on a CRT screen viewed at 57 cm. Gamma correction was employed to reduce CRT non-linearities, the refresh rate was 75 Hz. The stimulus aperture was $25° \times 25°$ with a 2.5° fixation mark in the center. Stimulus contrast was 15% with a mean luminance of 42 cd/m^2. Three different patterns were employed (Fig. 1): a sinusoidal grating, a "barcode grating" (sometimes described as one-dimensional noise), and a random dot pattern. The elementary dot size of the random dot pattern and the minimum bar width of the barcode grating were the same as half the period of the sine wave grating, which was 0.84°. The Fourier spectra of the patterns, computed for a cross-section along the direction of motion, are also displayed in Fig. 1. During the motion phases, patterns were drifting with a speed of 15°/s.

All nine possible combinations of adapting and test patterns were assessed: Each pattern served as adapting pattern in one experimental block with all three patterns as test stimuli. The adapting pattern was moving rightwards for 2200 ms. Then the test pattern appeared, but remained stationary for 500 ms before it started to move for 300 ms in either the same or the opposite direction. The resulting motion duty-cycle, i.e. the duration of the (adapting) motion divided by the total trial duration, ensured strong adaptation (Hoffmann et al., 1999) to build up over the first few trials. The type and direction of the test pattern was randomized. In separate blocks, the same stimulus sequence, but with a stationary adapting pattern, was used to obtain a low-adaptation baseline recording. The whole sequence of blocks was repeated in reversed order with the adapting pattern moving leftwards.

2.2. Recording

Ten subjects with normal or corrected-to-normal visual acuity (decimal acuity >1.0) took part and gave

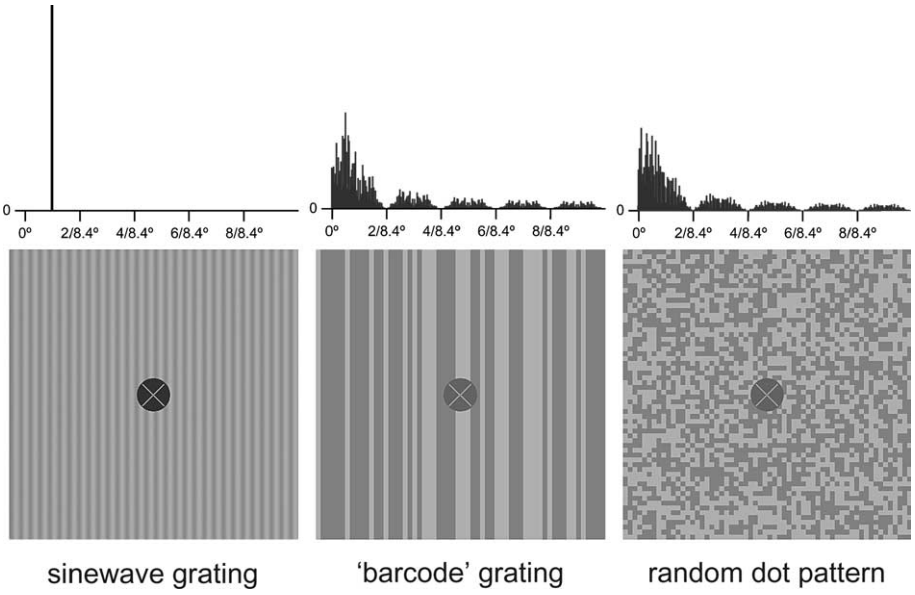

Fig. 1. Examples of all three stimulus patterns used. Stimulus size was 25° × 25°. Above each pattern, the Fourier spectrum, computed for a cross-section along the direction of motion (i.e. horizontal), is displayed. The spectra of the barcode pattern and the random dot pattern are identical except for random differences between particular instances of the respective pattern types.

their informed consent. Visual evoked potentials were recorded from Oz (located at the occipital pole) and OTL and OTR (5 cm to the left and right of Oz) as commonly used in motion VEP studies (e.g., Kuba & Kubová, 1992). 'Linked ears' served as reference. Additionally, the EOG was measured to detect eye blinks with a threshold criterion of 100 μV. Recording started after the first five trials when subjects had reached an adapted state. Signals were amplified, band-pass filtered at 0.3–70 Hz, digitized with a sampling rate of 500 Hz and written to disk for off-line analysis. Preliminary averages of the VEP and EOG were also displayed online to assess the recording quality. About 90 artifact-free trials were obtained for each adaptation/test condition.

2.3. Data analysis

Artifact-free trials were pooled according to stimulus conditions and averaged after being low-pass filtered at 20 Hz. Motion-onset VEPs often show a high degree of lateralization, which is not consistent between subjects (Andreassi & Juszczak, 1982). Therefore, for each subject, the occipito-temporal electrode (OTL or OTR) was chosen which produced the largest N2 amplitude averaged over all three baseline conditions. As in previous studies (Hoffmann et al., 1999; Maurer & Bach, 2003), this 'virtual' electrode was named OT*. All further analysis was done for OT* and Oz. The mean signal from 100 ms before to 50 ms after the stimulus onset served as zero level estimate.

The N2 amplitude values were used for statistical evaluation. They were taken as the voltage at the local minimum in the 130–200 ms time range. Due to the superposition of various VEP components (cf. Section 1), this value can be non-negative in some cases, in particular after adaptation. Subsequently, the N2 amplitudes corresponding to the different adaptation conditions will be denoted as follows: $A_{\rightarrow}$, baseline amplitude (unadapted); $A_{\rightrightarrows}$, amplitude after isodirectional adaptation; $A_{\leftrightarrows}$, amplitude after antidirectional adaptation. From these, the amplitudes of the N2 subcomponents were computed: $A_{\rightarrow} - A_{\leftrightarrows}$ represents 'flicker adaptation', which is not direction-specific. Direction-specific motion adaptation is given by $A_{\leftrightarrows} - A_{\rightrightarrows}$. The residual response is equal to the amplitude after isodirectional adaptation, i.e. $A_{\rightrightarrows}$.

The direct effects of adaptation and test patterns were assessed with Geisser-Greenhouse-corrected ANOVAs. The effects of using the same rather than different patterns for adaptation and test (subsequently labeled 'SAME' and 'DIFFERENT', respectively) were assessed with Student t tests. Estimation of significance levels was based on a sequential Bonferroni adjustment (Holm, 1979).

3. Results

Grand mean VEPs for all stimulus conditions are depicted in Fig. 2. Baseline recordings show clear N2 deflections in all conditions. Antidirectional adaptation causes a moderate reduction of N2 amplitude. A stronger decrease is found for isodirectional adaptation.

An overview of the effects of adaptation and test pattern and SAME vs. DIFFERENT adaptation is given in

Table 1 for all three subcomponents of the N2 deflection. The main significant effects are as follows:

Flicker adaptation (Fig. 3, left): At OT*, the random dot adaptation pattern yields 80% more adaptation than the other adaptation patterns. At Oz, SAME conditions cause on average 63% more adaptation than DIFFERENT conditions.

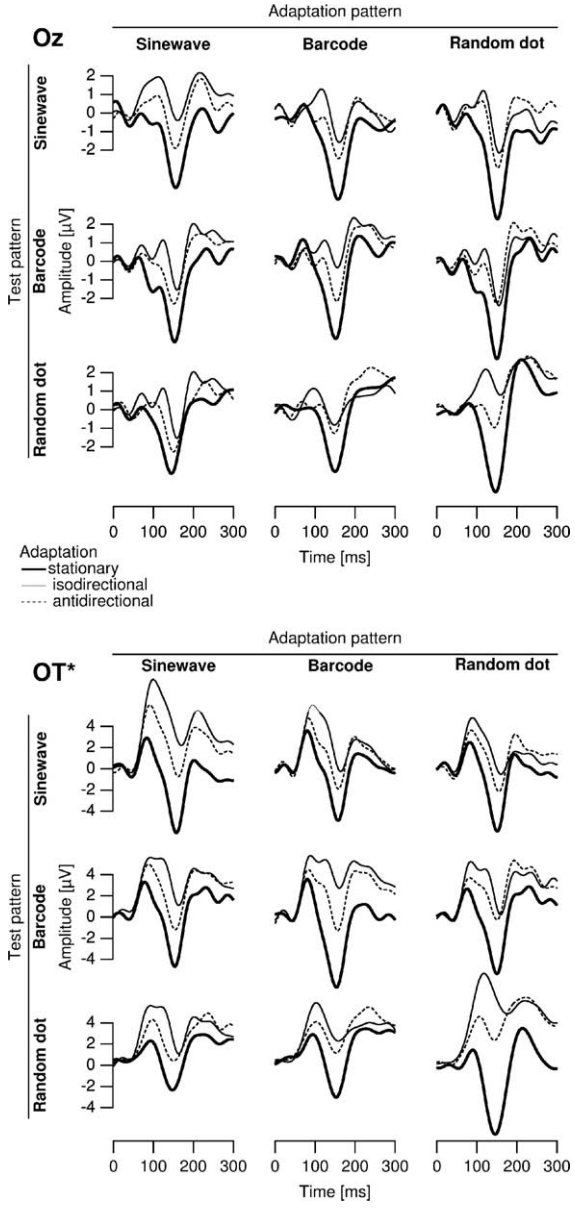

Fig. 2. Grand means for all conditions. The top panel shows Oz results, the bottom panel shows OT* results. Columns represent different adaptation patterns, rows represent test patterns. SAME conditions are located on the diagonal. Each triplet of curves consists of VEPs obtained with stationary (baseline), isodirectional, and antidirectional adaptation. The baseline N2 amplitudes are consistently largest. With one exception, the smallest amplitude was obtained when adaptation and test direction were identical. Note the different scaling of the Oz and OT* curves.

Table 1
P values for the effects of different factors on the various subcomponents of the N2 deflection as defined by their adaptability

Factor	Site	Flicker	Motion	Residual
		$A_{\rightarrow} - A_{\leftrightarrows}$	$A_{\leftrightarrows} - A_{\rightrightarrows}$	$A_{\rightrightarrows}$
Test pattern	Oz	0.44	0.18	0.0001^{**}
	OT*	0.53	0.80	0.0002^{**}
Adaptation pattern	Oz	0.0003^{**}	0.53	0.76
	OT*	0.0001^{**}	0.12	0.56
SAME vs. DIFFERENT	Oz	0.0002^{**}	0.0007^{**}	0.0001^{**}
	OT*	0.23	0.0030^{*}	0.0003^{**}

For the factors 'adaptation pattern' and 'SAME vs. DIFFERENT', the data was pooled across different test stimuli. Significance levels are based on a sequential Bonferroni adjustment. They are indicated in standard notation (global critical values: $^{*}\alpha = 0.05$; $^{**}\alpha = 0.01$).

Motion adaptation (Fig. 3, center): At both recording sites, considerably more adaptation is found in SAME as compared to DIFFERENT conditions (Oz, +138%; OT*, +144%).

Residual response (Fig. 3, right): The random dot test pattern produces the smallest (i.e. most positive) response, on average more than 5 μV less than the response to the barcode pattern. At both recording sites, responses in SAME conditions were 2.2 μV smaller.

Fig. 4 shows the response composition of SAME and DIFFERENT conditions, averaged across all three patterns. The amplitude obtained with antidirectional adaptation is approximately equal for both conditions. The residual response is larger with DIFFERENT adaptation, while the unadapted response at Oz is larger with SAME adaptation.

4. Discussion

All three test patterns evoked typical motion-onset responses. After isodirectional adaptation, amplitudes were more reduced than after antidirectional adaptation, as shown by earlier studies (Göpfert et al., 1984; Heinrich & Bach, 2003; Hoffmann et al., 2001). As schematized in Fig. 4, there are two main adaptation effects which cause a reduction in N2 amplitude. We propose that our experimental results may be disentangled as follows.

Flicker adaptation: The difference between the unadapted and the antidirectional conditions represent the flicker component (gray area in Fig. 4). It is obvious that the major part of the VEP evoked by motion onset does not represent veridical motion mechanisms, since its adaptation is not selective for direction (cf. Maurer & Bach, 2003). Flicker adaptation is similarly effective for both SAME and DIFFERENT conditions. This interpretation is supported by the near-identical amplitudes after anti-directional adaptation for both SAME and

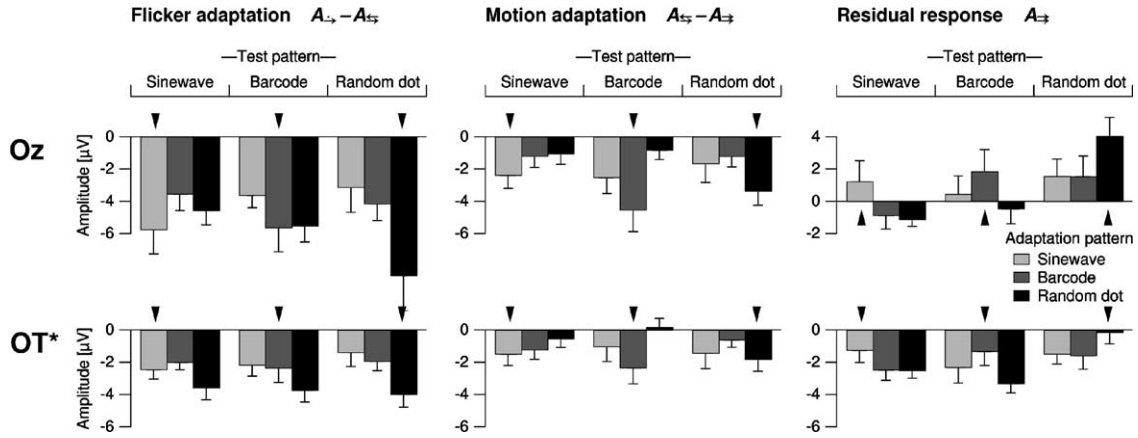

Fig. 3. Subcomponents of the N2 deflection. From left to right, the response portions affected by flicker adaptation and by motion adaptation as well as the residual response are displayed. Oz and OT* results are presented in the top and bottom row, respectively. Each group of 3 bars represents the values obtained with the same test pattern, but three different adaptation patterns. SAME conditions are marked by a triangle.

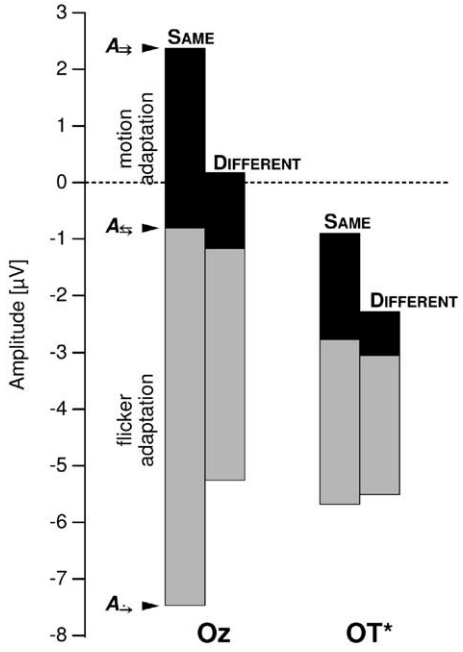

Fig. 4. Composition of the N2 component for SAME and DIFFERENT adaptation at both recording sites. Motion adaptation (direction specific) and flicker adaptation (not direction specific) are represented by black and grey, respectively. The response obtained with antidirectional adaptation ($A_{\leftrightarrows}$) is approximately equal for both conditions. The residual response ($A_{\rightrightarrows}$) at both sites and the unadapted response ($A_{\rightarrow}$) at Oz differ between SAME and DIFFERENT conditions.

DIFFERENT conditions (marked $A_{\leftrightarrows}$ in Fig. 4). The difference between unadapted amplitudes, though surprising at a first glance, can be explained by local luminance adaptation induced by the stationary pattern in the 'unadapted' conditions. This would primarily affect the SAME conditions where the pattern does not change before the test motion starts. The motion onset then evokes a larger flicker response as bright parts of the pattern move into dark-adapted regions of the visual field and vice versa. In DIFFERENT conditions, this effect only occurs at a subset of stimulus locations while the opposite effect occurs at other locations, where bright parts of the pattern move into light-adapted regions and only elicit a small flicker response.

Motion adaptation: Motion adaptation in the DIFFERENT condition is less complete than in the SAME condition, as reflected by the differences in the upper end of the black areas in Fig. 4. The almost 2.5-fold stronger adaptation in SAME conditions suggests that different moving patterns activate partly disjunct neural populations. This is the main finding of the present study.

When contrasting this rather strong finding with the literature, we encounter diffuculties which we cannot resolve at this stage:

(1) Assuming that the N2 reflects MT activity (Probst et al., 1993) this seems not consistent with reports that MT neurons are speed-selective irrespective of the pattern (Perrone & Thiele, 2001). However, speed selectivity in MT does not exclude the possibility of pattern effects due to adaptation at earlier stages. Area V3/V3A might also contribute to the N2 response (Schellart et al., 2004). Based on the size of the effect, though, it seems likely that a considerable part of the amplitude reduction in the DIFFERENT condition actually reflects MT activity.
(2) The present results are also in contrast to recent psychophysical findings by Fang and He (2004) who did not find substantial effects of the adaptation pattern on the motion after-effect, but report large effects of the test pattern. They used three types of patterns: sinusoidal gratings, squarewave gratings and squarewave gratings with scrambled phase. While they did not perform a full 3×3 design, they found that squarewaves as test produced the smallest aftereffect regardless of adapting pattern.

Comparing sinusoids and the barcode pattern, the present results are in line with those of Cameron et al. (1992) or Bex et al. (1996) who found spatial tuning of the motion aftereffect. But on these grounds one would not have predicted that the barcode pattern and the random dot pattern are ineffective cross-adaptors, because they have identical spectra in the direction of motion (Fig. 1, top). Not only do the response magnitudes differ, but there is less adaptation in the DIFFERENT conditions. Possible explanations might include effects of large receptive fields on the effective spatial spectrum, and the lack of motion streaks (Burr, 2000; Geissler, 1999; Kourtzi, 2004) in the case of moving barcode patterns. The accessibility of the motion-streak concept via evoked potentials might be a promising area to explore.

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